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Carsten K.W. De Dreu & Jörg Gross

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Between-group attack and defence in an ecological setting: insights from non-human animals

Andrew N. Radford¹, Susanne Schindler¹ & Tim W. Fawcett²

¹*School of Biological Sciences University of Bristol, UK*

²*Centre for Research in Animal Behaviour, University of Exeter, UK*

Correspondence: +44 (0) 117 3941197

andy.radford@bristol.ac.uk

susanne.schindler@bristol.ac.uk

t.w.fawcett@exeter.ac.uk

http://www.bio.bris.ac.uk/research/behavior/Vocal_Communication/home.html

<http://www.bristol.ac.uk/biology/people/susanne-schindler/overview.html>

<http://www.timwfawcett.com>

Abstract

Attempts to understand the fundamental forces shaping conflict between attacking and defending groups can be hampered by a narrow focus on humans and reductionist, oversimplified modelling. Further progress depends on recognising the striking parallels in between-group conflict across the animal kingdom, harnessing the power of experimental tests in non-human species and modelling the eco-evolutionary feedbacks that drive attack and defence.

Main text

De Dreu and Gross (D&G) rightly address a fundamental simplification of theoretical and empirical research on between-group conflict; the prevailing assumption that competing groups are equivalent is unrealistic in many ways. By considering key differences between attackers and defenders, how those differences might arise, and the strategic, social and psychological consequences, D&G provide an elegant initial exploration of the topic. However, we argue that two crucial extensions are needed for a

full understanding of this neglected aspect of sociality and its implications for human society: a broader taxonomic perspective and a more ecologically and evolutionarily relevant modelling approach.

First, D&G focus almost exclusively on humans, ignoring similar conflicts in other social animals. Contests between rival groups are commonplace across taxa from insects to primates (Batchelor & Briffa 2011; Hardy & Briffa 2013; Kitchen & Beehner 2007; Radford 2003; Thompson et al. 2017), and non-human between-group conflict parallels the human scenarios discussed by D&G in many respects. For instance, fighting usually arises over a resource (e.g. food, mates, territory) already held by one group (Christensen & Radford 2018; Kitchen & Beehner 2007), and so there is an inherent role asymmetry between attackers (seeking to gain the resource) and defenders (seeking to protect that resource from usurpation). For a given pair of groups, especially in territorial species where contests between neighbours are common, which group is attacking and which is defending can change across time (birds: Radford & du Plessis 2004; mongooses: Thompson et al. 2017; primates: Wilson et al. 2012), and repeated interactions can influence subsequent behaviour even in the absence of recent conflict (Radford 2011). Moreover, collective-action problems can arise whether the resource being competed for is of direct benefit to all or only a subset of group members (Schindler & Radford 2018; Willems et al. 2015). As a final example, home-field advantage—where defenders are disproportionately more successful than attackers—has been regularly recorded in non-human group-living species (primates: Crofoot et al. 2008; mongooses: Furrer et al. 2011; birds: Strong et al. 2018).

Considering only one species limits development of ideas about the causes and consequences of between-group conflict for several reasons. Conflict is a powerful selective force across taxa, but some of the conclusions drawn by D&G are likely to apply only to humans. For example, D&G emphasise the need for means to motivate and coordinate collective attacks. Whilst sanctioning systems (e.g. punishment) and rewards may occur in many species with respect to participation in between-group conflict (Arseneau-Robar et al. 2016, 2018; Radford et al. 2016), the need for additional institutional arrangements is almost certainly a uniquely human construct. Considering more species would allow the relative importance of these different mechanisms to be teased apart. Even for researchers interested only in human behaviour, our shared evolutionary history and clear parallels with other species mean there is value in taking a broader taxonomic perspective. That is particularly true because whilst D&G showcase experimental approaches that can be used with humans, these are necessarily artificial scenarios. Experimental testing of between-group conflict, including in natural conditions, is more feasible in non-human species: it is possible to stage contests (ants: Batchelor & Briffa 2011; fish: Brounjes et al. 2016) and to simulate the recent (e.g. faecal presentations; mongooses: Christensen et al. 2016) and current (e.g. vocal playbacks; mongooses: Furrer et al. 2011; birds: Radford 2005; primates: Wilson et al. 2001) presence of rivals. Experimental

testing alongside further theoretical development is clearly going to be key when advancing D&G's ideas concerning attack vs defence in between-group conflict.

A second limitation concerns the simple game-theory models presented by D&G, which do not capture important ecological and evolutionary forces shaping between-group conflict in real-world settings. D&G conceptualise the interaction between an attacking group and a defending group as a one-shot, simultaneous ('sealed bid') game with no variation between groups (in size, resources, fighting ability, etc.), only two possible actions (or a one-dimensional investment in the conflict) and a pay-off matrix with fixed parameter values. This ignores the effect of future interactions on the value of the current conflict (the 'shadow of the future' alluded to by D&G), the rich array of behavioural options available to group members (including retaliation after an attack) and the powerful feedbacks arising from the decisions of other groups. These are not trivial details, but can fundamentally alter conflict outcomes (McNamara 2013). Work in evolutionary biology has emphasised the importance of embedding games in a wider ecological context, where the pay-offs from alternative actions emerge from the stable strategic solution to the game, rather than being specified in advance as arbitrary fixed values (Houston & McNamara 2005). D&G also ignore how contest decisions depend on uncertainty about the fighting strength of rivals, which has an important effect on aggressive tendencies (Enquist & Leimar 1983; Johnstone 2001; McNamara & Houston 2005) and is likely to promote strategies for gathering information before launching an attack. Such considerations are particularly relevant when there are repeated interactions, which are ignored in D&G's one-shot games but are likely to be common between neighbouring groups and others in close proximity, where the threat of retaliation is high and dynamic changes in fighting strength may drive the pattern of conflict.

Whilst all models are necessarily an abstraction of reality, ignoring the wider ecological or cultural context in which between-group conflict takes place impairs our ability to derive valid, testable predictions. We urge researchers to take a broader, ecologically informed view of attack and defence, considering the rich array of examples across the animal kingdom. This is especially important when applying theoretical insights to our own species: basing conclusions for human society on oversimplified, reductionist models is potentially dangerous, because it could misguide policy makers and politicians into accepting a limited room for manoeuvre.

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